

GEOGRAPHICAL VARIATION IN  
*PACHYBRACHIS NIGRICORNIS*  
(COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

A taxonomic revision indicates that *Pachybrachis nigricornis* (Say) is a polymorphic species (morphologically as well as chromatically). This species includes 3 polytopic subspecies, *P. n. nigricornis*, *P. n. difficilis* Fall, and *P. n. autolycus* Fall; and one monotypic subspecies, *P. n. carbonarius* Fall. The subspecies differ most notably by color characters. Stepwise discriminant analysis indicates that the subspecies are taxonomically distinct when segregated by a character index. Pigmentation in *P. n. autolycus* is light and its distribution corresponds with dry climates, which facts agree with those of *P. othonus sioux* Balsbaugh, a sibling species of *P. n. autolycus*. *P. n. nigricornis* is dark and shiny, but it too occurs in arid areas. Fall's Group D key to vittate species has been modified to reflect the new nomenclature changes and to include the black subspecies of *P. nigricornis*.

When analyzing geographic variation in the polymorphic species *Pachybrachis othonus* (Say), Balsbaugh (1973) discovered the existence of sibling species, i.e. "morphologically similar or identical natural populations that are reproductively isolated" (Mayr 1971), in *P. o. sioux* Balsbaugh and what at that time was known as *P. autolycus* Fall. Such a phenomenon had been recognized earlier in lady beetles by Dobzhansky (1933) who stated that, "Homologous varieties of different species may be more similar to each other in appearance than the different varieties of the same species." In addition to the many other examples of animal sibling species that Mayr (1965) has cited, Vavilov (1922) also recognized that large groups of related plant species and genera often exhibit parallel series of homologous patterns.

The discovery that *P. o. sioux* and *P. autolycus* were sibling species led us to conduct further studies on infraspecific-geographic variation in the latter species. Names for the color forms in the *autolycus*-complex include: *P. nigricornis* (Say, 1823); *P. carbonarius* Haldeman, (1849); *P. carbonarius* var. *janus* Fall, (1915); *P. autolycus* Fall, (1915); *P. autolycus* var. *difficilis* Fall, (1915); and *P. autolycus* var. *wahsatchensis* Fall, (1915).

METHODS

For an indication of conspecificity, male genitalia of several specimens of all color forms were dissected and compared (Figs. 1-5).

For an indication of taxonomic distinction and to evaluate geographic variation, 10 characters were used and coded in character states as follows:

1) Pronotal surface texture: (1) specimens with pronotal surface strongly alutaceous and (2) beetles with pronotal surface smooth or only slightly alutaceous.

2) Pronotal punctation density: (1) dense punctation and (2) less dense punctation.

3) Size of pronotal punctures: (1) pronotal punctures much less coarse than elytral punctures and (2) punctures nearly as coarse as elytral punctures.

4) Pronotal coloration: (1) totally black pronotum, (2) pronotum black but with anterior edges lighter, (3) pronotum with paired basal and medial anterior spots, and (4) pronotum with large yellow areas and a distinct black M-shaped mark.

5) Elytral coloration: (1) totally black, (2) black with reddish yellow lateral edges, (3) with sutural and interrupted mid-elytral vittae, and (4) with yellow stripes as wide or wider than black stripes.

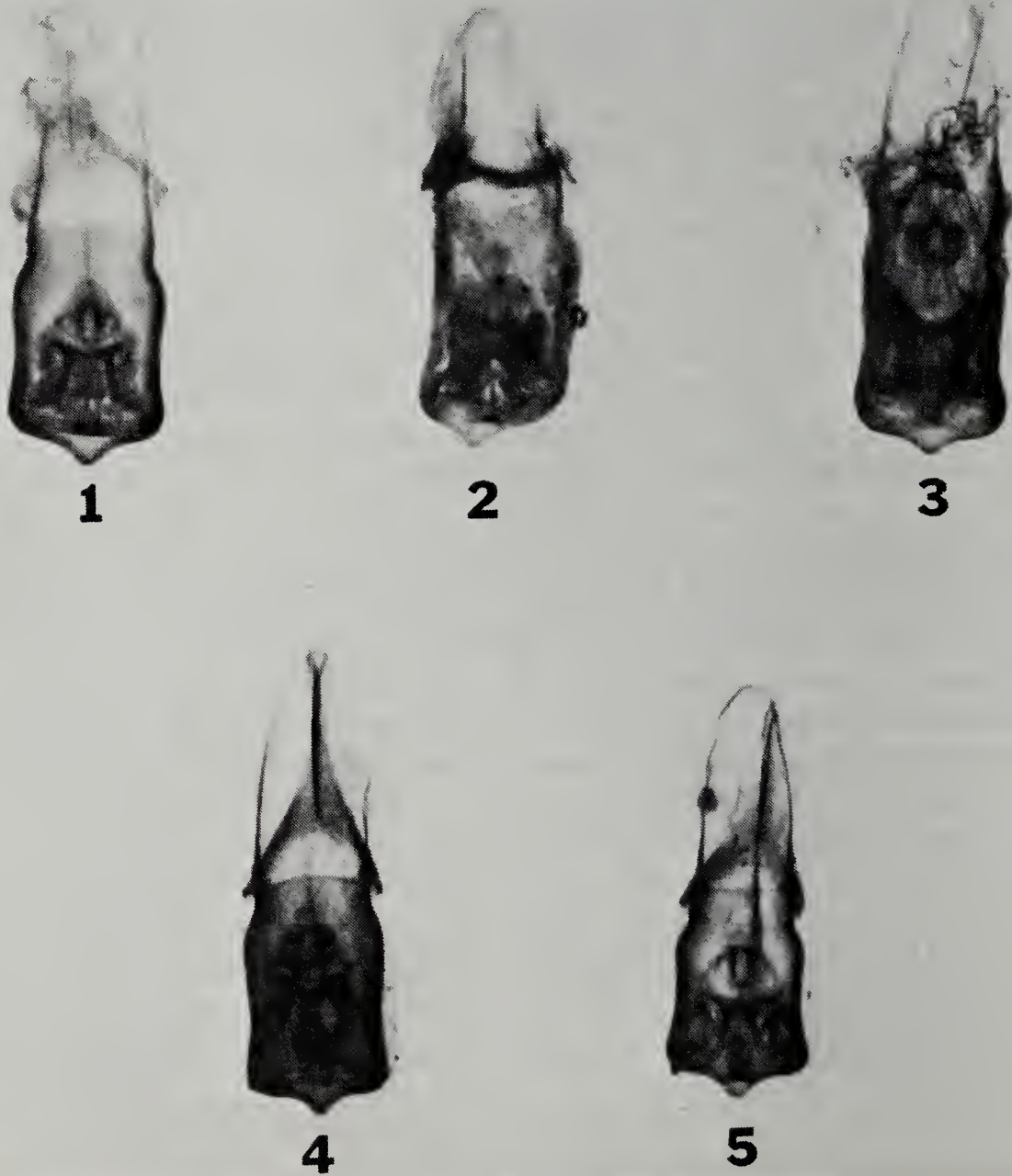


Fig. 1-5. Dorsal views of aedeagi: 1) *Pachybrachis nigricornis nigricornis* (Say); 2) *P. n. carbonarius* Haldeman; 3) *P. n. difficilis* Fall, formerly var. *difficilis*; 4) *P. n. difficilis* Fall, formerly var. *wahsatchensis* Fall; 5) *P. n. autolytus* Fall.



6) Pygidial coloration: (1) all black, (2) black with paired yellow spots, and (3) apical area entirely yellow.

7) Character index: a character index for each specimen was comprised of the sum of the values of the 6 preceding characters.

8) Elytral width: maximum width across both elytra.

9) Elytral length: length from front edge of elytron at humerus to posterior edge of elytron at apex, in a line parallel to the elytral suture.

10) Elytral ratio: elytral width/elytral length.

Measurements were made with an ocular grid. A total of 865 specimens was used in this study. All of the above character values were used in a step-wise discriminant analysis.

Correlation of characters with distribution was attempted. Based on experience with *P. othonus* (Balsbaugh 1973), political states were assigned code numbers, one per state for those states east of the 100th meridian. States through which the 100th meridian passes and the mountain states immediately to the west of them were subdivided into 2 or 3 areas, because greater variation was expected in these areas.

#### SYNONYMY AND DIAGNOSES

*Pachybrachis nigricornis nigricornis* (Say)  
(Fig. 1, 6, 7)

*Cryptocephalus nigricornis* Say, 1823, Journ. Acad. Nat. Sci. Philadelphia 3:436-437. (Neotype, Fig. 6).

*Pachybrachis carbonarius* var. *janus* Fall, 1915. Trans. Amer. Ent. Soc. 41:462-463. (Holotype, Fig. 7). **New synonymy.**

*P. n. nigricornis* is distributed chiefly in the Great Plains states and provinces (Fig. 12). Say (1823) listed the type locality as "Missouri", which meant the Missouri Territory and included areas west to the Rockies. It is not found in the present state of Missouri; rather its range is continuous in Nebraska, South Dakota, North Dakota, and Saskatchewan, with discontinuous pockets in Oregon, Washington, Idaho, Alberta, Colorado, Kansas, and Arkansas.

Inasmuch as Weiss and Ziegler (1931) indicated that Say's collection, including his American types, had been destroyed, we are designating a neotype for *P. nigricornis* in order to synonymize the name with certainty with Fall's *P. carbonarius* var. *janus*. Based on current knowledge of distribution of *P. nigricornis*, there are 3 areas where Say traveled in 1820 from which he may have collected specimens of this species: In Nebraska, along the westward route of the Long Expedition up the Platte River; in Colorado near Long's Peak; and in Arkansas along the Arkansas River, the eastward route of the Expedition. We have selected the neotype from Boulder, Colorado, an area very near to, if not on the actual route of the Long Expedition. On June 30, 1820, for the first time, the Long Expedition saw Long's Peak which is near Boulder (Weiss and Ziegler, 1931, p. 77).

We are proposing the new synonymy of *P. n. nigricornis* (Say) and *P. carbonarius* var. *janus* Fall, based on comparison of our neotype for the former with Fall's holotype of var. *janus*. Fall (1915, p. 462-463) was just as uncertain as to how to treat this color form as he was the 2 varieties of



*P. autolytus* that he also described, viz. *difficilis* and *wahsatchensis*. Concerning var. *janus*, he stated: "This form lies exactly between typical *carbonarius* and *nigricornis* and merges into both so gradually that I am as yet completely unable to draw the dividing lines."

The following description is based on the neotype of *Cryptocephalus nigricornis* Say; see also Say (1823).

*Description:* Body 1.35 times as long as wide; widest at humeri, sides more or less parallel but slightly concave just behind the humeri and tapered in gradual arch at posterior end; black, dorsal surface shiny, without pubescence, pygidium and venter with dense short whitish pubescence.

*Head:* Black, alutaceous; frons densely punctate with short seta in each puncture; vertex more sparsely and less coarsely punctate, punctures not setose; labrum rufous; eyes (female) separated by 0.6 times distance from labral suture to occiput. Antennae black, except basal 4 joints rufous on venter, length,  $1/2$  length of body.

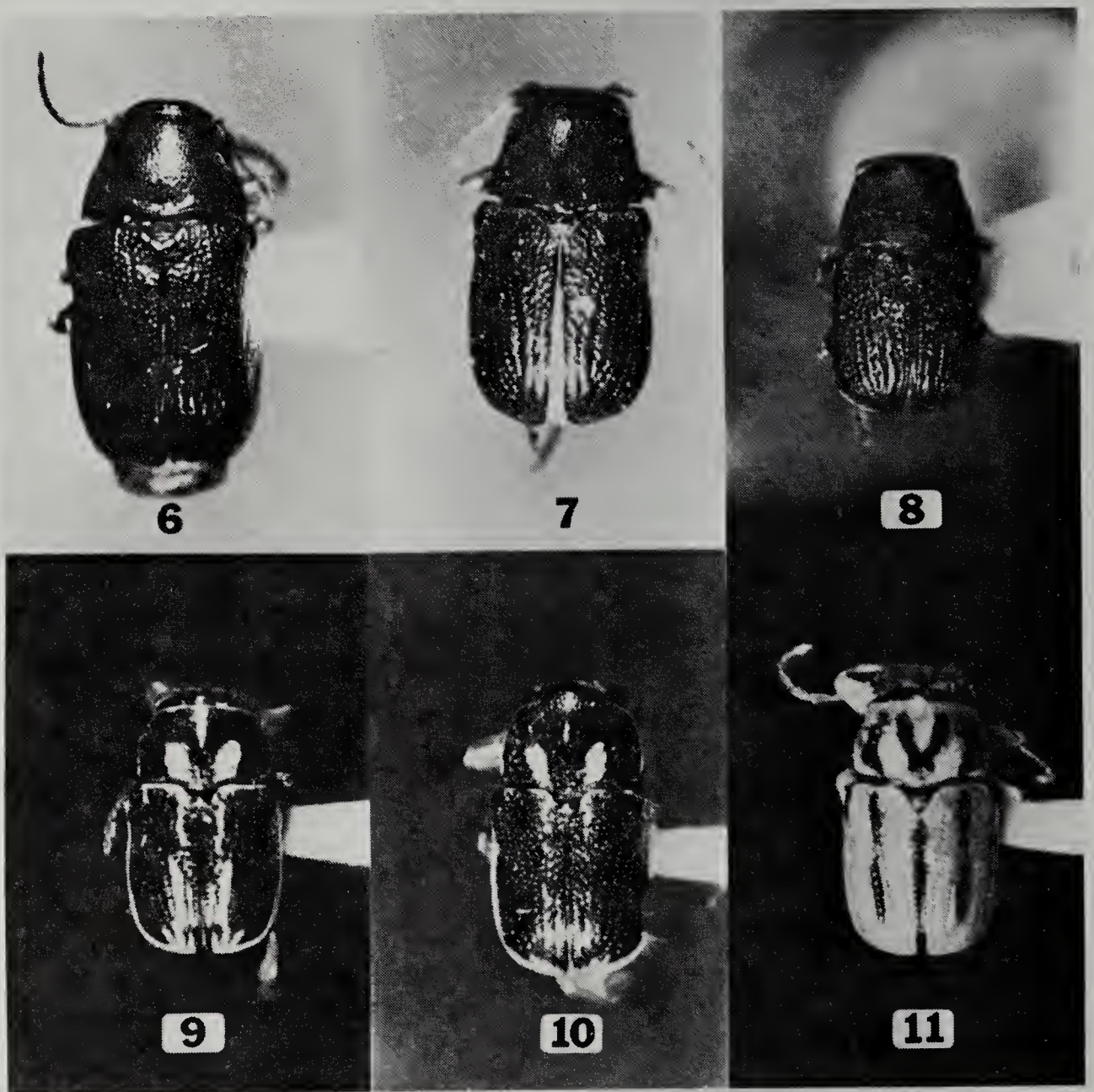


Fig. 6-11. 6) Neotype, *Cryptocephalus nigricornis* (Say) (= *P. n. nigricornis* (Say)); 7) Holotype, *P. carbonarius* var. *janus* Fall (= *P. n. nigricornis* (Say)); 8) Holotype, *P. carbonarius* Haldeman (= *P. n. carbonarius* Haldeman); 9) Holotype, *P. autolytus* var. *difficilis* Fall (= *P. n. difficilis* Fall); 10) Holotype, *P. a.* var. *wahsatchensis* Fall (= *P. n. difficilis* Fall); 11) Holotype, *P. autolytus* Fall (= *P. n. autolytus* Fall).



*Pronotum*: Black, shiny, but slightly alutaceous (more distinctly so than elytra); densely punctate. Lateral margins rufous but marginal bead black.

*Scutellum*: Black.

*Elytra*: Black, shiny, punctate, punctures in nearly regular striae; interstriae somewhat costate. Lateral margins, basal bead, and apex obsoletely rufous.

*Ventral Surface*: Black, densely setigerously punctate. Fifth abdominal sternite (female) with medial fovea. Legs black, except knees, tibiae and tarsi slightly rufous.

*Length*: 3.8 mm.

*Type data*: The neotype is a female. [Original probably was a female. Say gave its size as "less than three-twentieths of an inch" (= 3.81 mm).] Type locality: "Boulder, Colo. 5800', June 5, 1961, B. H. Poole." The neotype is deposited in the Canadian National Collection, Entomology Research Institute, Ottawa, Canada.

*Pachybrachis nigricornis carbonarius* Haldeman  
(Fig. 2, 8)

*Pachybrachis carbonarius* Haldeman, 1849, Journ. Acad. Nat. Sci. Philadelphia, Ser. 2, 1:260. (Holotype, Fig. 8)

*P. n. carbonarius* is distributed in the eastern half of North America (Fig. 12) west to Manitoba, the extreme eastern parts of the Dakotas, and south to eastern Texas. Southern Ontario and the Great Lakes are the northern boundaries and it extends south to central Mississippi, Alabama, Georgia, and Florida. Haldeman (1849) gave the type locality as "Southern".

*Description*: Body 1.69-1.80 times as long as wide; widest at humeri, sides more or less parallel; black or dark brownish black, dorsal surface dull, not shiny, without pubescence, pygidium and venter with dense short whitish pubescence.

*Head*: Black, alutaceous, frons densely punctate with short seta in each puncture; vertex more sparsely and less coarsely punctate, punctures not setose; labrum rufous. Antennae black, basal joints rufous on venter, 1/2 length of body in female, about 3/4 length of body in male.

*Pronotum*: Black, alutaceous, dull; densely punctate; occasionally lateral margins rufous.

*Scutellum*: Black.

*Elytra*: Black or brownish black, usually lighter in color than the pronotum. Punctate in nearly regular rows; interstriae somewhat costate. Punctures larger than those of pronotum.

*Ventral Surface*: Black, densely setigerously punctate. Fifth abdominal sternite of female foveate. Legs black, except knees, tibiae, and tarsi slightly rufous.

*Length*: 2.4-3.6 mm.

*Hosts*: Series of specimens have been taken on wild strawberry and *Desmodium*, and a single specimen was recorded taken on *Quercus* sp.

*Pachybrachis nigricornis difficilis* Fall  
(Fig. 3, 4, 9, 10)

*Pachybrachys autolytus* var. *difficilis* Fall, 1915, Trans. American Ent. Soc. 41:459. (Holotype, Fig. 9).

*Pachybrachys autolytus* var. *wahsatchensis* Fall, 1915, Ibid. 41:459-460. (Holotype, Fig. 10). **New synonymy.**

Distribution of this subspecies is very odd (Fig. 12). It occurs primarily in western North America and so far as current collection samples indicate it is found in disjunct populations in Oklahoma, Texas, New Mexico, Arizona, Colorado, Utah, Wyoming, Montana, Idaho, Oregon, Washington, British Columbia, Alberta, Saskatchewan, and Manitoba. It also is found in eastern North America. Fall (1915) recorded Tyngsboro, Massachusetts, as type locality for *P. a. difficilis*. It occurs in northern New York, Quebec, eastern Ontario, and the northern-most areas of the south peninsula of Michigan.

New synonymy has been proposed after comparison of Fall's holotypes. Fall (1915), when describing the varieties *difficilis* and *wahsatchensis*, mentioned their close relationship, indicating that they differ primarily through the absence of intrahumeral yellow spots in *wahsatchensis*. He also stated that "it is far from unlikely that both *wahsatchensis* and *difficilis* are the more usual forms of the rare *nigricornis*." Had Fall compared the aedeagi (Figs. 1, 3, 4) he probably would have concluded that these forms are conspecific.

By way of clarification, we have observed an error or a mixup in labels attached to 2 paratypes of *P. a. difficilis* belonging to the U. S. National Museum. Two paratypes of *difficilis* from "Ashfork, Ar." were labeled as paratypes of "*autolycus* var. *wahsatchensis* Fall." These are probably those specimens of *difficilis* collected by Barber and Schwartz, mentioned in Fall's (1915) revision. We have left these 2 specimens with the errors, as we found them, but have added our own determination labels.

*Description:* Body 1.76-1.88 times as long as wide; widest at humeri (males) or at mid area of elytral length (females); elytra black with yellow vittate interruptions, varying from nearly completely black with submarginal and subsutural vittae to black with submarginal, subsutural and mid-elytral yellow vittae; dorsal surface shining; pygidium and venter with dense short whitish pubescence.

*Head:* Black, with yellow areas mesad of both upper and lower ocular lobes and on clypeus; frons densely punctate with short seta in each puncture; vertex more sparsely and less coarsely punctate, these punctures not setose; labrum yellow. Antennae black, basal joints rufous on venter, 1/2 length of body in females, about 3/4 length of body in males.

*Pronotum:* Black, with mid apical, paired basal, anterior and lateral margins yellow; shining, densely punctate.

*Scutellum:* Black.

*Elytra:* (See general description).

*Ventral Surface:* Black, densely setigerously punctate. Fifth abdominal sternite of female foveate. Legs black except yellow spots on apical ends of mid and hind femora.

*Length:* 2.8-3.8 mm.

*Hosts:* Host plants have not been recorded for this subspecies.

*Pachybrachis nigricornis autolycus* Fall  
(Fig. 5, 11)

*Pachybrachys autolycus* Fall, 1915, Trans. American Ent. Soc. 41:458-459. (Holotype, Fig. 11).

*P. n. autolycus* is a subspecies occupying a dry habitat (Fig. 12). It occurs more or less continuously in Kansas, Oklahoma, and northeastern Texas, with smaller disjunct populations or individuals in Arkansas, Missouri,



Iowa, southwestern Illinois, North Dakota, South Dakota, Alberta, Nebraska, New Mexico, Arizona, and Colorado.

Fall (1915 p. 460) indicated that *autolycus* "... approaches *othonus*" (*sensu stricto*) and Balsbaugh (1973) demonstrated that it and *P. o. sioux* Balsbaugh were sibling species.

*Description*: Body 1.75-1.85 times as long as wide; widest at humeri (males) or at mid area of elytral length (females); elytra yellow with the suture and 2 vittae per elytron black; lateral-most vitta frequently interrupted; dorsal surface shiny to dull alutaceous; pygidium and venter with dense short whitish pubescence.

*Head*: Black with yellow areas on clypeus and mesad of eyes, usually more yellow than *P. n. difficilis*; frons densely punctate with a short seta in the punctures; vertex more sparsely and less coarsely punctate, these punctures not setose; labrum yellow. Antennae brown, basal joints lighter, 1/2 length of body in female and about 3/4 length of body in male.

*Pronotum*: Yellow with distinct black M-shaped mark, varying to minutely alutaceous, densely punctate in black areas.

*Scutellum*: Black.

*Elytra*: (See general description).

*Ventral Surface*: Black, fifth abdominal sternite margined apically with yellow, fifth abdominal sternite of female with medial fovea. Legs yellow, apexes of hind tibiae darker. Pygidium black basally, with paired contiguous yellow apical spots and a pair of smaller lateral ones.

*Length*: 2.6-3.8 mm.

*Hosts*: A collection by M. W. Sanderson of a large series on *Desmodium* at Valmeyer, Illinois, May 24, 1950, very nicely reinforces our belief in the conspecificity of *P. n. autolycus* and *P. n. carbonarius* on biological grounds, as well as morphologic. This plant was reported as a host for *P. n. carbonarius* by an unknown collector, in Crawford Co., Arkansas.

#### KEY TO SUBSPECIES OF *P. nigricornis* AND THEIR CLOSE RELATIVES

Fall (1915) presented a key to 159 species of *Pachybrachis* by recognizing groups of species based chiefly on coloration. It is now quite evident that such groupings pose great problems for identifiers since polymorphic species have been demonstrated (Balsbaugh, 1973). A new key to all species of North American *Pachybrachis* is needed, but such must await further analyses by species-groups, such as that done in this paper. Nevertheless, we present the following key, modified from Fall's Group D key, which encompasses chiefly vittate forms, but also now the black subspecies of *P. nigricornis*.

1. Punctuation of elytra very irregular ("confused") ..... 2
- 1'. Punctuation of elytra arranged in nearly regular series (less conspicuously so in *P. picturatus*) ..... 6
- 2(1). Terminal spurs of front tibia wanting or rudimentary; last segment of maxillary palpus scarcely differing between sexes; punctuation coarser and denser; southern and southeastern United States ..... *P. viduatus* (Fab.)

- 2'. Terminal spur of front tibia normally developed; last segment of maxillary palpus more widely truncate in male; punctation finer and less dense ..... 3
- 3(2'). Eyes in male separated by distance evidently less than twice length of basal antennal segment; elytra bivittate, outer stripe rarely if ever continuous, interrupted or not, in form of 1, 2 or 3 spots ..... *P. bivittatus* (Say)
- 3'. Eyes in male separated by distance at least twice length of basal antennal segment ..... 4
- 4(3'). Elytra of some specimens with single narrow vitta, with or without faint traces of lateral spots, but usually destitute of markings; submarginal stria very irregular; eyes in male separated by twice length of basal antennal segment, or little more. California ..... *P. sublimatus* Fall
- 4'. Elytra each with single broad discal vitta; eyes separated by 2.50 to 3.00 times length of basal antennal joint ..... 5
- 5(4'). Eyes in female less widely separated than by their own vertical length; submarginal stria nearly regular. California and Oregon ..... *P. circumcinctus* Crotch
- 5'. Eyes in female more widely separated than by their own vertical length; submarginal stria more irregular. California ..... *P. consimilis* Fall
- 6(1'). Prothorax densely punctate, punctures more or less strigose, especially laterally; with smooth median line extended posteriorly from anterior margin, but not reaching basal margin ..... 7
- 6'. Prothorax punctate, but punctures less dense, not strigose; anterior medial line of various widths, or absent ..... 9
- 7(6). Elytra vittate ..... 8
- 7'. Elytra not vittate; yellow with sutural bead, humeri and punctures black ..... *P. othonus pallidipennis* Suffrian
- 8(7). Pronotum with pair of yellow spots at base, one on either side of medial line ..... *P. othonus sioux* Balsbaugh
- 8'. Pronotum without basal spots ..... *P. o. othonus* (Say)
- 9(6'). Elytra entirely black, or black with narrow subsutural vitta, and sometimes with lateral and apical margins yellow ..... 10
- 9'. Elytra with predominating ground color yellow ..... 12
- 10(9). Elytra entirely black or dark brown ..... 11
- 10'. Elytra black with narrow subsutural vittae, intrahumeral basal spots, or lateral and apical margins yellow ..... *P. nigricornis difficilis* Fall
- 11(10). Pronotum densely punctate, alutaceous; usually blacker in color than elytra ..... *P. nigricornis carbonarius* (Haldeman)
- 11'. Pronotum less densely punctate, shining to minutely alutaceous; usually of same color as elytra ..... *P. n. nigricornis* (Say)



- 12(9'). Elytron yellow with single discal black vitta ..... 13
- 12'. Elytron yellow with suture or sutural bead and 2 discal  
vittae on each black or brownish ..... 14
- 13(12). Elytra yellow with single narrow, often imperfect or sub-  
obsolete, median black vitta; and humeri and posterior  
spot black; New Mexico, Arizona ..... *P. umbraculatus* Suffrian
- 13'. Elytra yellow with single straight sharply defined but  
narrow black vitta and black humeri. North and South  
Carolina ..... *P. picturatus* Germar
- 14(12'). Front claws of male not enlarged ..... 15
- 14'. Front claws of male distinctly enlarged; lustre dull, outer  
elytral vitta confined to 7th and 8th interspaces.....  
..... *P. pawnee* Fall
- 15(14). Surface sculpture of head and pronotum more or less aluta-  
ceous (very fine and visible only on head and towards sides  
of pronotum in some examples of *P. nigricornis autolytus*)..  
..... 16
- 15'. Integument polished; alutaceous sculpture not present ex-  
cept occasionally very faintly on head ..... 17
- 16(15). Pronotum strongly transverse, more closely punctate.....  
..... *P. nigricornis autolytus* Fall
- 16'. Pronotum moderately transverse, more sparsely punctate;  
always distinctly alutaceous. Florida, Georgia, South Caro-  
lina, North Carolina, District of Columbia and New Jer-  
sey ..... *P. litigiosus* Suffrian
- 17(15'). Outer elytral vitta beginning on 7th and 8th interspaces,  
and ending on 6th and 7th ..... 18
- 17'. Outer elytral vitta confined to 7th and 8th interspaces; me-  
dian pronotal stripe conspicuously V-shaped ..... 19
- 18(17). Median pronotal stripe narrowly V-shaped; size smaller  
(2.7-3.8 mm). Texas, Kansas..... *P. dubiosus* LeConte
- 18'. Median pronotal stripe not V-shaped but merely dilated  
slightly anteriorly, dilated portion usually with very  
narrow more or less obscure paler line; size larger (3.7-  
4.4 mm). Nebraska, Kansas, Texas, Colorado ..... *P. virgatus* LeConte
- 19(17'). Vittae black. Arizona, Utah, Colorado, Texas ..... *P. v. vau* Fall
- 19'. Vittae obsolescent, usually brownish. Texas.....  
..... *P. vau imperfectus* Fall

## RESULTS AND DISCUSSION

Taxonomic treatment in a revision such as this—as in any systematic study—is to a great extent a matter of subjective interpretation. In this paper, we have chosen to combine 3 separate species and to elevate one of Fall's former varieties to subspecific rank. Two of Fall's varieties are placed in synonymy. We conclude that *P. nigricornis* is a polymorphic

species (morphologically as well as chromatically) which includes 3 polytopic and 1 monotypic subspecies. Mayr (1969) stated that "The only alternative to it [the polytopic subspecies] is not to recognize any subspecies in such a species." We choose to recognize subspecies in *P. nigricornis*, rather than just 1 species with variants, because the variations are taxonomically and geographically distinct.



Fig. 12. Distribution of the subspecies of *P. nigricornis*. Solid black = *P. n. nigricornis*; grey = *P. n. carbonarius*; parallel lines = *P. n. difficilis*; dots = *P. n. autolytus*.



Mayr (1969) defined a subspecies as "an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species." Disagreement as to what constitutes "taxonomic differences" is at the crux of subjectivity. The subspecies of *P. nigricornis* differ most obviously by color characters. Such characters probably are determined by a complex of genes. Lus, as cited by Dobzhansky (1933), determined that color patterns in *Adalia bipunctata* and *A. decimpunctata* were controlled by at least 8 multiple allelomorphs, and that another gene determined only pronotal patterns. Multiple genes and allelomorphs likely control chromatic differences in *Pachybrachis* spp. also, and therefore the subspecies we recognize probably reflect variations tied to more than a single gene.

The following results were obtained from numerical taxonomic treatment. Table 1 shows the means and standard deviations for the 10 characters used. Table 2 is a within groups correlation matrix which is produced by a stepwise discriminant analysis. A correlation matrix is a symmetrical table of correlation coefficients of each variable in a set of variables with every other one. Of the characters that we used and of the manner in which we assigned values to them, none were totally independent. All characters, including the character index (#7), measured characters (#8, #9) and the ratio of the latter 2 (#10) were used in the discriminant analysis. The character index (#7) was used as a means of making subspecies groups. Four

Table 1. Means and standard deviations for 10 characters used in discriminant analysis of *P. nigricornis*.

Character	<u>P. n.</u> <u>nigricornis</u>		<u>P. n.</u> <u>carbonarius</u>		<u>P. n.</u> <u>autolytus</u>		<u>P. n.</u> <u>difficilis</u>	
	M	SD	M	SD	M	SD	M	SD
(1) Pronotal surface texture	1.56	0.50	1.10	0.30	1.74	0.44	1.74	0.44
(2) Pronotal punctation density	1.45	0.50	1.09	0.28	1.60	0.49	1.62	0.49
(3) Pronotal punctation size	1.32	0.47	1.03	0.17	1.57	0.50	1.17	0.38
(4) Pronotal coloration	1.66	0.64	1.01	0.09	3.64	0.48	3.00	0.34
(5) Elytral coloration	1.98	0.31	1.03	0.17	3.96	0.21	3.02	0.25
(6) Pygidial coloration	1.04	0.19	1.02	0.31	2.80	0.42	1.63	0.60
(7) Character Index	9.02	1.14	6.25	0.53	15.32	1.20	12.17	1.13
(8) Elytral width	17.97	2.00	17.58	1.84	17.83	1.98	18.05	1.97
(9) Elytral length	21.87	2.52	20.88	2.32	21.17	2.51	21.86	2.48
(10) Elytral ratio	0.82	0.04	0.84	0.04	0.84	0.03	0.82	0.07

Table 2. Within groups correlation matrix of 10 characters used in evaluating variation in *P. nigricornis*.

	1	2	3	4	5	6	7	8	9	10
1	1.0000									
2	.2360	1.00								
3	-.0134	.1088	1.00							
4	-.0230	-.0276	.0140	1.00						
5	-.1679	-.1956	-.1772	.2362	1.00					
6	.0067	-.0113	-.0316	.2118	.2020	1.00				
7	.4679	.5085	.3763	.5328	.1842	.4420	1.00			
8	.0526	-.0930	-.0576	.0474	.0675	.1097	.0482	1.00		
9	.0925	-.0656	-.0386	.0401	.0339	.0991	.0673	.9220	1.00	
10	-.1013	-.0113	-.0763	.0161	.0625	-.0086	-.0557	.0377	-.2643	1.00

groups were assumed, viz. *P. n. carbonarius* which were those specimens having a character index of 6-7, *P. n. nigricornis* 8-11, *P. n. difficilis* 12-13, and *P. n. autolycus* 14-17. The separate character values had been chosen so that low values were dark specimens and at the opposite extreme, high values were light specimens. Punctuation and textural gradations were correspondingly assigned as well. Table 2 lists the means and standard deviations for the 10 characters used.

Fig. 13 is a discriminant analysis plot, based on the 10 characters and recognizing 4 populations. Of the 865 specimens used in the study, only 48 were misidentified; thus, 94.45 percent were correctly grouped by use of the character index. Thus the 4 subspecies are taxonomically distinct.

A discriminant analysis utilizing all 10 characters and 4 groups, based on geographic criteria was not conclusive. We feel that the geographic analysis was faulty because assignment of specimens to a geographic region, i.e. states or portions of states, was not a fine enough grouping. Fig. 12 accurately described the distribution of the subspecies of *P. nigricornis*, based on present material.<sup>1</sup> We have utilized the "75% rule" in compiling this map.

Pigmentation: Accumulation of pigments in animals of humid regions with a corresponding depigmentation in arid regions has been recognized for years, having been first verbalized as a rule by Gloger in 1833 who applied it to birds. This rule also holds true for many invertebrates. Some of the correlations of humidity-pigmentation in insects have been observed or demonstrated by Zimmermann (1931) in Vespidae; Netolitzky (1931) in Carabidae; Dobzhansky (1933) in Coccinellidae; Ford (1937), Hovanitz (1941), LeGare and Hovanitz (1951) in Lepidoptera; Balsbaugh (1973) in *P.*

<sup>1</sup>Distribution records are on file and are available to interested persons. They are not published because of the archival nature of these data.



*othonus* (Chrysomelidae) and Hardwick and Lefkovitch (1973) in Noctuidae. However, Zuska and Berg (1974) cite many examples among poikilothermic animals for which this rule does not hold. In fact, there are cases of clinal progressions in the opposite direction.

Of the 4 subspecies of *P. nigricornis*, *P. n. autolytus* is the most lightly pigmented. It is found in the arid areas of Nebraska, Kansas, Oklahoma, etc. Hardwick and Lefkovitch (1973) stated that "the paler forms of *E. declarata* (Noctuidae) are characteristic of areas of low rainfall in the Great Basin and on the High Plains", which agrees greatly with the distribution of many *Pachybrachis* spp. (Balsbaugh 1973 and unpublished observations of the senior author). However, the many examples of *P. n. nigricornis* from areas of low rainfall in northwestern South Dakota and northwest into Saskatchewan and Alberta agree with the opposite correlations mentioned by Zuska and Berg (1974).

The phenotypes expressed in the various subspecies of *P. nigricornis* are adaptations to suit their particular environments. The discontinuous distributions of the polytopic subspecies, viz. *P. n. nigricornis*, *P. n. autolytus* and *P. n. difficilis*, most likely resulted from independent evolution of similar phenotypes which adapt their members to similar environmental pressures, rather than from these subspecies having evolved through disruption of a former more continuous range, or through macroleaps of dispersal. Voous (1951) showed that when species of birds from humid areas of Venezuela colonized arid islands in the West Indies, they independently evolved similar phenotypes, i.e. greater paleness and other features.

Zuska and Berg (1974) suggested that activity levels of poikilothermic animals are critically dependent on body temperatures and therefore temperatures of heliotherms are far more dependent on heat received from the sun than on metabolic heat. Intake of sunlight energy in them is greatly influenced by body color. Therefore dark pigments are advantageous in cold climates because they absorb radiant energy better. Dobzhansky (1933),

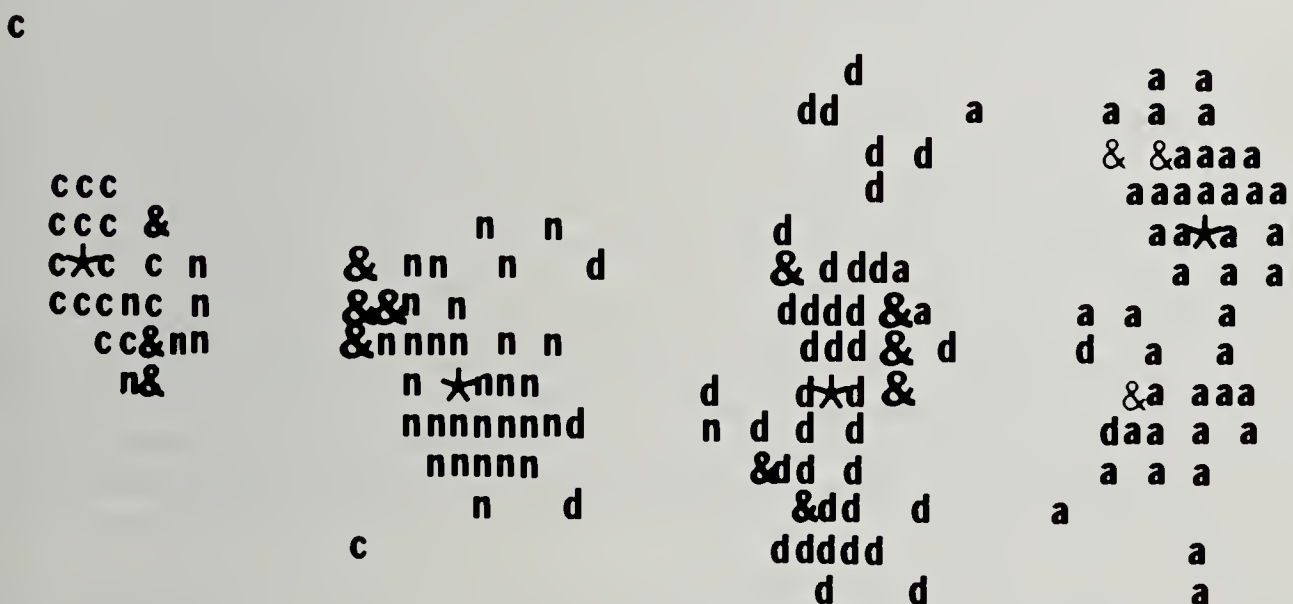


Fig. 13. Discriminant analysis plot for 10 characters when four groups are assumed. a = *P. n. autolytus*; c = *P. n. carbonarius*; d = *P. n. difficilis*; n = *P. n. nigricornis*; & = multiple entries and \* = group means.

on the other hand, said that pigmentation "... seems to be related to the degree of humidity, and possibly, to the temperature prevailing in a given region ... The role of humidity seems to be more important than that of temperature since the increase of pigmentation is observed in some species (of Coccinellidae) in humid but otherwise so different countries in northeastern Siberia, Japan, northern Europe, Abyssinia and Himalya."

In South Dakota, the annual average mean temperature, except for the Black Hills, decreases from south to north. To the contrary, annual average rainfall declines from east to west. Balsbaugh (1973) demonstrated that in *P. othonus*, in South Dakota, pigmentation is correlated with rainfall amounts, i.e. darker specimens correspond with areas of greater rainfall. In *P. nigricornis*, it appears that temperature and humidity may both be important as environmental selective pressures.

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